THE LIFE ZONE SYSTEM

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M^{*}. Holdridge m^{*} a envoyé en réponse à mon article ; a Conceptions modernes en bicclimatologie et classification des formations végétales a (Adamsonia 5,3 : 1963) la note suivante en me demandant de la publier dans Adamsonia, ce que je fais bien voloniters. J'aurai d'autres occasions de revenir plus tard sur un sujet qui est de toute première importance pour l'écologie des rézions tropicales.

A. Aubréville

On pages 297-306 of Fascicule 3, Tome V of the journal Adansonia, Prof. A. AURKËVILLE has published a discussion of both the potential evapotranspiration concept of C. V. ThowsTuwATE and my life zone, bioecological classification system. Relative to the latter, I have put together the following notes to clarify some of the specific questions raised.

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The life zones of my system as defined in precise numerical ranges of mean annual precipitation, mean annual biotemperature and potential evapotranspiration ratio on the chart are only first order divisions of the climates and vegetational groupings on the land areas of our planet.

The chart, originally published in 1947, was constructed mainly on the basis of preceding experience and publications of many ecologists, elimatologists, hotanists, pedologists and other scientists with some contribution from my own findings in the tropics. Since the chart was first assembled with only temperature and precipitation values, my particular contributions were the use of a new value, that of *biolemperature*, for showing temperature relations, the finding that significant guide lines of biotemperature and precipitation values and the arrangement of a set of hexagons, as determined by the guide lines, so as to deline natural units in the field as well as clearly show their climatic relationships to other life zones.

Although the chart is presented in two dimensions, it actually represents a threedimensional figure, an important aspect not mentioned by M. AURAÉVILLE. At higher elevations the biotemperature and precipitation values are the same as those for lifezones of cooler latitudinal regions but are different primarily because of distinctive annual ranges of temperrature. These upper altitudinal life zones are indicated by placing both the life zone, latitudinal region and altitudinal belt names before the life zone, as for example: Tropical Montane Wet Forest Life Zone. For such upper belts, the region may be determined by calculation of the corresponding sea-level biotemperature from the local adiabatic rate of temperature change with altitude.

Previously, I had supposed that a satisfactory mean annual biotemperature could be obtained by eliminating below 00 C. temperatures and thus obtaining a mean annual average of the positive Celsius temperatures only. More recent investigations within the tropics have shown clearly that above 30° C. temperatures must also be eliminated or discounted heavily in the calculation of the mean annual biotemperature. We are exploring this aspeet of temperature with plant physiologists who have in the past found some indication of a drop in net photosynthesis above about 30° C. The new formula for biotemperature will provide a satisfactory separation of the Subtropical region, or outer tropics, from the Tropical Region, or inner teopics.

Following development of the chart from precipitation and biotemperature values alone it was reasoned that the third set of coordinates must reprensent the interaction of the other two guide line coordinates, the result of which could only be humidity or moisture. Study of pedological literature indicated that the value which offered the best fit for representation of humidity was that of the potential evapotranspiration ratio of Thomstruwarrs.

In spite of whatever may be said about Thousruswarre's method of calculation of potential evapotranspiration or his own attempted application of the same to regional classification. Thornthwaite did make an extremely valuable contribution to climatology and ecology with his concept of potential evapotranspiration. Evolution has molded the elements of the natural vegetation at any point on the world to not only thrive under the existing temperature conditions, but also to be in complete adjustment with the relation of the actual precipitation to the potential evapotranspiration at that temperature, and in accordance with the moisture holding capacity of the soil and the local atmospheric conditions.

Thus, in the semi-arid province, potential evapotranspiration varies from 2 to 4 times the precipitation. The natural vegetation has evolved to withstand drought conditions of several months. The experience of Becuź, which M. AumavirLie cites of transplanting elements of such a vegetation to an area with a potential evapotranspiration ratio of 5 to 1 resulted in death or poor growth of the plants. The results do not appear to detract from the concept of potential evapotranspiration, as it should be interpreted, but rather seem to confirm the natural significance of humidity provinces and life zones.

As mentioned earlier, the life zones are only first order natural divisions of vegelation. These divisions may be recognized in the field by one who has conscientiously applied himself to learning the life zone system. However, the vegetation of each life zone comprises a number of distinct vegetation associations, which make up the second order level of the life zone system. Finally, the actual successional stage of an assocition or any type of land-use which man is applying to a portion of an association area constitutes the third level division or that of the actual status of the vegetation.

Although he has mentioned the association level in a footnote on page 305, Prof. Aupnéville has admitted that he does not understand what I mean by atmospheric associations. Actually, I define 4 types of associations. The elimatic association is the one association in each life zone with a zonal soil and zonal climate. By the latter, is meant a normal rainfall distribution in relation to the total precipitation and without any special atmospheric conditions. The name of the climatic association is inserted in each hexagon of the chart.

The atmospheric associations, which may comprise several for each life zone, are those which are significantly different from the climatic association due to additional azonal modifications in climate such as strong winds, abundant mists, or pronounced variation in the seasonal precipitation pattern. On the semantic level one may object to the term "Atmospheric". This was selected primarily because the distinctive vegetations are often due to local atmospheric conditions, as well as to purposely differentiate such climatic features from the global climatic factors of biotemperature, mean annual precipitation and humidity.

Edaphic associations are those which are significantly different from the climatic due to toopgraphy, drainage, parent material, age or the like, which latter have given rise to intrazonal or azonal soils. One may find, to be sure, associations which are edapho-stmespheric due to a combination of factors, such as a beach thicket on a sandy soil subject to strong and often salt-laden brezes.

There are, in addition, hydric associations where the soil is covered with water for all or most of the year. However, these are usually not considered in the mapping of land vegetation.

Based on the previous explanation of associations, it should be apparent that to some extent Prof. Aturn'sruth: thas confused life zones with associations and even with third order divisions. Thus, his statements that there are three dense forests with an annual precipitation of from 1500 to 1800 mm and areas with more than 2000 mm where forests no longer exist are perfectly compatible with the life zone system. As a matter of fact, we have at least 6 different forest associations in Costa Rica within the Tropical Dry Forest Life Zone, within approximately the 1500 to 1800 mm range. These are edaphic associations which can readily be explained by soil or drainage conditions and can all be readily recognized as belonging to the Tropical Dry Forest Life Zone. We also have many areas in Tropical America with over 2000 mm of precipitation where forests no longer exist, but these are obviously third category divisions due to land use practices. The life zone concept can be of real value for both orientation and explanation. The wide range in associations within a life zone ranging from those on excessively draimed soils with an extended dry season to those on ferilie soils with a raised water table and with an extended wet season may be confusing to the person who does not understand the first order category of the life zone. On the other hand, with the knowledge that these are all within one life zone, the effects of the second order factors are readily apparent and explosible.

Stand height, number of tree species per unit area and relative abundance of palms are some of the characters which differentiate comparable association vegetations of the several life zones which are often grouped together as the "Tropical Rain Forest". Indigenous peoples and native agriculturalists also demonstrate in their patterns of land use an acknowledgement of the differences between the several life zones which, surprisingly, are considered by many ecologists to comprise only one vegetation or climatic unit. The chart differentiates nine life zones within the "Tropical Rain Forest". They are the low elevation Moist, Wet and Rain Forest Life Zones of both the Subtropical and Tropical regions plus the three life zones of the same humidity provinces in the Premontane altitudinal belt of the Tropical region. An examination of the chart should clearly indicate that such divisions are only logical extensions into the tropics of the humidity province divisions generally accepted by ecologists in the more adequately studied temperate zone regions. Although such a division of the "Tropical Rain Forest" was made with some trepidation at first, because it disagreed with genereal ecological literature, subsequent, detached observations in the field have borne out the soundness of the division into nine life zones.

Although species groupings are helpful locally in demarcating life zones and associations, the system is basically physiogromic. This permits comparisons and relations on a world-wide basis regardless of biogeographical regions with their essentially distinct taxonomic groupings. Personal experimere in Southeastern Asia and Tropical Africa has shown me that it is just as easy to recognize the natural life zone units in these regions as in the Americas.

Both life zones and associations within the former may be separated on a physiognomic basis. However, with only a limited number of workers, we admittedly have not had the facilities to provide objective physiognomic measures to cover the life zones of the world. The subjectivity in mapping life zones where adequate climatic data is not available is analogous to the recognition of the family in plant taxonomy from plant material without fruits or flowers.

Both the life zones and plant families are natural units defined in the former by climatic ranges and in the latter by flower and fruit characters. In each case experience usually permits subjective identification even when the objective characters for exact classification are not available. A lack of ability by many workers to make such subjective identifications in either of the two fields should not be considered a sound basis for criticism of the objectively defined natural divisions of either the plant family or the life zone,

In the preceding, I have attempted to clarify without going into any great detail that the file zone system does not ignore any of the factors which affect vegetation. These are all taken into account in the threelevel categories of classification. If M. AUMENTLLE closes to judge the life zone system on the basis of the chart for the first order categories alone, that is his privilege, but it is hardly a just appraisal of the total system. If ecology is to progress as it should to a precise science, we must advance beyond opinions alone and discuss evaluations based on measurements of vegetation correlated with climatic and pedologic data.

As for mapping, I am in complete agreement with Prof. AUBATULE that it would be most desirable to have maps showing vegetation distribution down to the third category or that of actual conditions. However, economics is still a controlling factor and one can only proceed to that mapping level for which support is available. Under the circumstances, a first-category or life zone map helps considerably in showing the value of ecological classification, assists in planning and carrying out comparative research and should help to stimulate the sponsorship of the highly desireable but much more expensive second-and third-category mapping programs.

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